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Vegetation carbon stocks driven by canopy density and forest age in subtropical forest ecosystems

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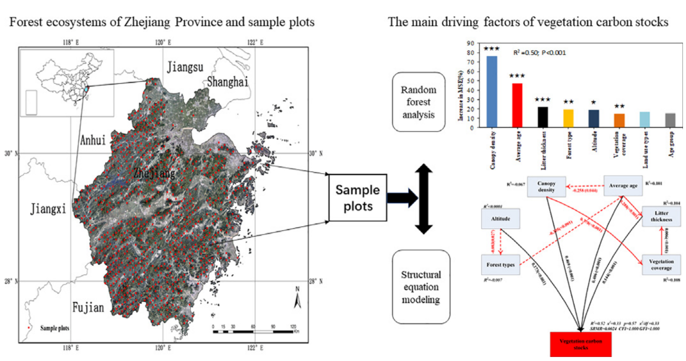
HIGHLIGHTS

- Random Forest analysis combined with SEM to evaluate the abiotic and biotic driving factors effects on vegetation carbon stocks.
- Canopy density and forest age were the most crucial driving factors.
- Provides new insights into the potential response of subtropical forest ecosystems carbon sequestration to climate change.

GRAPHICAL ABSTRACT



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ABSTRACT

Subtropical forests play an important role in global carbon cycle and in mitigating climate change. Knowledge on the abiotic and biotic driving factors that affect vegetation carbon stocks in subtropical forest ecosystems is needed to take full advantage of the carbon sequestration potential. We used a large-scale database from national forest continuous inventory in Zhejiang Province, and combined the Random Forest analysis (RF) and structural equation modeling (SEM) to quantify the contribution of biotic and abiotic driving factors on vegetation carbon stocks, and to evaluate the direct and indirect effects of the main driving factors. The RF model explained 50% of the variation in vegetation carbon stocks; canopy density accounted for 17.9%, and forest age accounted for 7.0%. Moreover, the SEM explained 52% of the variation in vegetation carbon stocks; the value of standardized total effects of canopy density and forest age were 0.469 and 0.327, respectively, suggesting that they were the most crucial driving factors of vegetation carbon stocks. Since the forests in our study were relatively young, the forests had a large potential for carbon sequestration. Overall, our study provided new insights into the sensitivity and potential response of subtropical forest ecosystems carbon cycle to climate change.

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1. Introduction

Human activities, such as combustion of fossil fuels and deforestation, increase the concentration of atmospheric carbon dioxide (CO_2) that is one of the main causes of global climate change (IPCC, 2014). A large body of research indicates that forest ecosystems play an important role in the global carbon cycle. The capacity of forests for sequestering additional atmospheric CO_2 is one possible way to mitigate climate warming (Luyssaert et al., 2007; Pan et al., 2011; Xu et al., 2016). National carbon budgets have been calculated and carbon stocks estimated in regional forests (Canadell and Raupach, 2008; Chave et al., 2003; Chheng et al., 2016; Phillips et al., 2016), including tropical, subtropical, temperate, boreal, and bamboo forests (Chave et al., 2003; Houghton, 2005; Mao et al., 2016; Xu et al., 2011; Yen, 2016; Zhang et al., 2007; Zheng et al., 2008; Zhou et al., 2011). The subtropical forests are widely distributed and frequently disturbed by human activities. The total net ecosystem productivity (NEP) of East Asian monsoon subtropical forests was estimated to be 0.72 ± 0.08 Pg C yr^{-1}, which accounts for 8% of the global forest NEP. The average NEP value of subtropical forests is higher than those of Asian tropical forests, temperate forests, and forests at the same latitudes in Europe, Africa and North America (Yu et al., 2014). However, the effects of abiotic and biotic factors on vegetation carbon sequestration in large regional forest ecosystems are rarely studied. Thus, studying the driving factors of carbon sequestration in subtropical forests will significantly improve our knowledge of the terrestrial carbon cycle.

Previous studies have shown that the carbon sequestration ability of forest ecosystems is interactively driven by abiotic and biotic factors such as forest origin, forest age, forest type, geography, and soil environment. For instance, carbon stocks increased from 1.70 Mg C ha^{-1} in grasslands, 4.15 Mg C ha^{-1} in shrublands, 22.3 Mg C ha^{-1} in shrub forests, and 70.3 Mg C ha^{-1} in secondary forests to 142.2 Mg C ha^{-1} in primary forests in a chronosequence of natural vegetation in karst regions (Liu et al., 2016). In different ecological service forest types of Zhejiang Province, the mean biomass values were significantly different among evergreen broad-leaved forest, coniferous and broad-leaved mixed forest, pine forest, and Chinese fir forest (Zhang et al., 2007). Forest age is also a critical factor determining ecosystem carbon storage and fluxes. The rate of carbon storage changes declined with stand age and approached equilibrium during the later stage of stand development (Yang et al., 2011). Gray et al. (2016) suggested that the old and large trees are important carbon stocks, but play a minor role in additional carbon accumulation in Pacific Northwest forests. Wang et al. (2017) found that forest age was a dominant factor that modulated carbon turnover times, especially for vegetation. In a *Zanthoxylum bungeanum* plantation, the total forest ecosystem carbon storage increased with plantation age (Cheng et al., 2015). Research on the relationships between net primary productivity and stand age for several forest types confirmed the importance of forest age in estimating regional and global terrestrial carbon budgets (Wang et al., 2011). Besides forest type and forest age, vegetation coverage strongly determines the forest structure and plant growth, since it may also be important for vegetation biomass accumulation (Grytnes, 2000; Ji et al., 2009). An increased canopy opening increased the potential and variance of height growth (Madsen and Larsen, 1996), thereby increased the forest biomass.

The abiotic factors that affect forest carbon sequestration include altitude, slope, slope position, soil environment, and climate. Particularly, altitude, slope and aspect influence stand microclimate, which has both direct and indirect effects on aboveground biomass in forest ecosystems (Fotis et al., 2017). Environmental factors affect species distributions and abundances (Boerner, 2006; Fotis et al., 2017; Murphy et al., 2015), which in turn affect both physical and biological stand attributes, for example tree size distribution, leaf arrangement, and leaf physiological traits (Fahey et al., 2015; Fotis et al., 2017; Jucker et al., 2015). There may also have a direct effect on aboveground biomass by affecting soil moisture availability (Boerner, 2006); in wetter areas the aboveground biomass is commonly higher (Desta et al., 2004; Sharma et al., 2011). Zhang and Chen (2015) reported that nutrient availability may affect aboveground biomass by affecting stand structure. Altitude affects plant growth and productivity primarily through temperature effects (L. Xu et al., 2017), while slope through solar radiation, wind velocity and soil types (Moeslund et al., 2013). Fan et al. (2012) reported that the carbon stocks of Moso bamboo forests were significantly affected by slope aspect and slope position.

Some of the relationships between abiotic/biotic factors and aboveground biomass or productivity have been studied, yet the main driving factors and their contributions in subtropical forest ecosystems carbon sequestration are still uncertain. In this study, we collected data from 701 forest plots from subtropical forests in Zhejiang, China. We used Random Forest analysis to identify the main driving factors of vegetation carbon stocks, and then used structural equation modeling (SEM) to evaluate the direct and indirect effects of the main driving factors on vegetation carbon stocks. Both approaches provide complementary insights on the patterns that drive vegetation carbon stocks at a large scale. The main objectives of this study were to (1) quantify the contribution of each driving factor, (2) reveal the main driving factors of vegetation carbon stocks, and (3) evaluate the direct and indirect effects of the main driving factors on vegetation carbon stocks.

2. Materials and methods

2.1. Description of study area

The study area in Zhejiang Province (118°1′–123°10′ E, 27°6′–31°11′ N), on the southeast coast of China, covers approximately 105,500 km^2 (Fig. 1). The terrain varies from mountains with an average altitude of 800 m in the southwest, to hills in the central areas and alluvial plains in the northeast (Mao et al., 2017). The area has a subtropical monsoon climate with annual average precipitation of 1319.7 mm and annual average temperature of 15.6 °C. The primary vegetation types are coniferous evergreen, mixed coniferous, deciduous broad-leaved, and bamboo forests (Xu et al., 2018). The primary soil types are yellow and red soils (Chinese Soil Taxonomy), equivalent to Hapludult in the U.S. Department of Agriculture Soil Survey Manual (Soil survey Staff of United States Department of Agriculture (USDA), 1999). By the end of 2010, forests area in Zhejiang Province was 6.02 million ha, including 0.254 billion cm^3 of live stumpage, and accounting 60.63% of the total area (DFZP, 2011).

2.2. Sample plots and data collection

We collected data from 701 permanent sample plots that were designed and sampled following the national forest continuous inventory protocols. The east-west interval between adjacent plots was 6 km, the south-north interval was 4 km, and each plot covered an area of 800 m^2. In each plot, abiotic factors (slope, aspect, slope position, altitude, land use type and soil thickness) and biotic factors of tree (diameter at breast height (DBH), trees height, canopy density, forest type, forest origin, forest age, vegetation coverage, age group, humus layer thickness, litter thickness,vegetation coverage and ratio of C to N in leaf) were recorded from May to September in 2010 (Supplementary file 1). Based on the principles of Chinese vegetation regionalization (Hou et al., 1982) and the national forest continuous inventory protocols, we classified the sampled forests into six forest type groups: deciduous broadleaf forest (DBF), deciduous needle-leaf forest (DNF), evergreen broadleaf forest (EBF), evergreen needleleaf forest (ENF), bamboo forest (Bamboo), and needleleaf and broadleaf mixed forest (NBF). The shrub and herb characteristics (average height, average ground diameter and coverage) were measured from three randomly selected 2 m × 2 m quadrats in each plot.

The aboveground and belowground vegetation biomass in sample plots were estimated using forest biomass model designed by Yuan

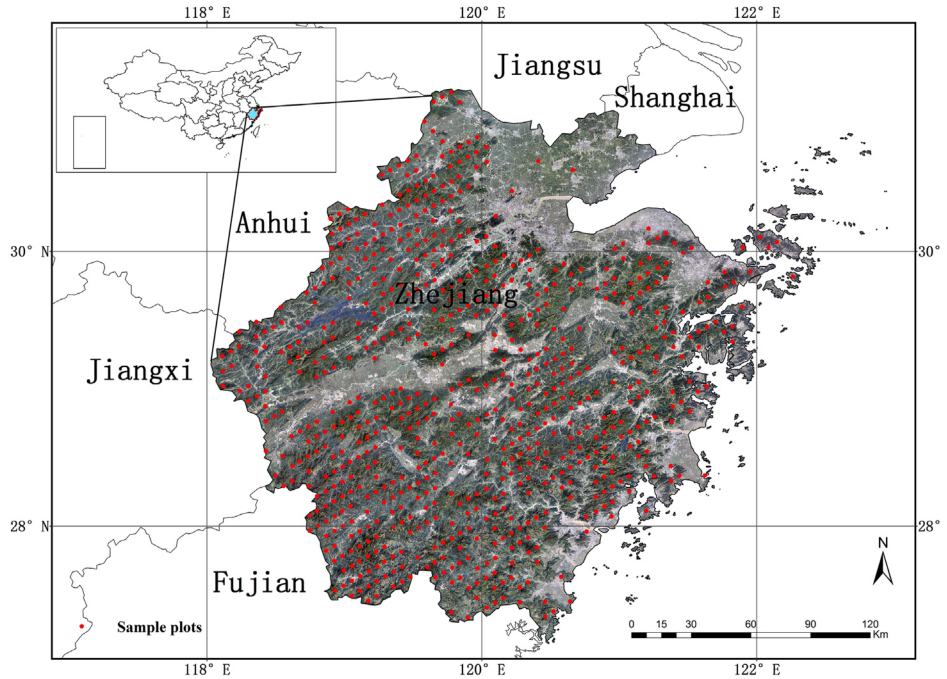

Fig. 1. Study sites and the distribution of sample plots.

et al. (2009), which was based on long-term practical measurements of forest vegetation in Zhejiang, including hard broadleaf, soft broadleaf, pine (*Pinus*), Chinese fir (*Cunninghamia lanceolata*), bamboo, shrub, and herb biomass models (Dai et al., 2018) (Table 1). The total vegetation biomass was a sum of biomass of each vegetation type. The total vegetation carbon stock was calculated by multiplying the total vegetation biomass per unit area (Mg ha^{-1}) with the carbon conversion coefficient (Tan et al., 2007; Ren et al., 2011; Tao et al., 2014; Zhang et al., 2007) (Table 1).

2.3. Data analysis

Statistical analyses were performed using R v3.2.1 (http://cran.r-project.org/). We calculated the carbon stocks in the sample plots, and used the average carbon stocks and the area of the forests to calculate the total carbon stocks. Kernel density estimation was used to estimate the distribution of carbon stocks in forests of different origin, type and age group. We used multiple regression analysis to determine the relationship between the carbon stocks and abiotic/biotic factors.

The main driving factors of vegetation carbon stocks among the abiotic and biotic factors were identified using a classification Random Forest analysis (RF) in the randomForest package (Liaw and Wiener, 2002). Random Forest is a novel machine-learning algorithm which extends standard classification and regression tree (CART) methods by creating a collection of classification trees with binary divisions (Delgadobaquerizo et al., 2016). The fit of each tree is assessed using 1/3 of the randomly selected data, which are withheld during its construction (out-of-bag cases) (Delgadobaquerizo et al., 2016). When the data for the predictor is randomly permuted, the increase in the mean square error (*MSE*) between observations and out-of-bag predictions is evaluated to determine the importance of each predictor variable. This accuracy importance measure is calculated for each tree and averaged over the forest (5000 trees). The parameters ntree, mtry and nodesize of RF approach in our study were 5000, 3 and 5, respectively. The significance of the model and cross-validated R^2 was assessed with 5000 permutations of the response variable (vegetation carbon stocks) using R package A_3. The significance of the importance of each driving factor was assessed by using R package *rfPermute* (Archer, 2013).

We used structural equation modeling (SEM) to evaluate the direct and indirect effects of the main driving factors on vegetation carbon stocks. Before constructing the SEM model, the collinearity of the factors were tested to eliminate factors with collinear relationship. The first step in SEM requires establishing a priori model based on known effects and relationship among the driving factors of forest growth and biomass accumulation (Supplementary file 2). The normality of the variables was tested, the variables were natural logarithm transformed and standardized. After data transformation, we parameterized our model and tested its goodness of fit using the Chi-square (χ^2) test, goodness-of-fit index (GFI), comparative fit indexes (CFI), and standardized root

Table 1
Vegetation biomass models and carbon conversion coefficients of each vegetation type.

Type of vegetation	Root model	Crown model	Stem model	Total model	Carbon conversion coefficient
Hard broadleaf 1	$W = 0.0549H^{0.1068}D^{2.0953}$	$W = 0.0980D^{1.6481}L^{0.4610}$	$W = 0.0560H^{0.8099}D^{1.8140}$	$W = W_R + W_C + W_S$	0.4834
Hard broadleaf 2	$W = 0.2470H^{0.1745}D^{1.7954}$	$W = 0.2860D^{1.0968}L^{0.9450}$	$W = 0.0803H^{0.7815}D^{1.8056}$	$W = W_R + W_C + W_S$	0.4914
Pine	$W = 0.0417H^{-0.0780}D^{2.2618}$	$W = 0.1377D^{1.4873}L^{0.4052}$	$W = 0.0600H^{0.7934}D^{1.8005}$	$W = W_R + W_C + W_S$	0.4596
Chinese Fir	$W = 0.0617H^{-0.1037}D^{2.1153}$	$W = 0.0971D^{1.7814}L^{0.0346}$	$W = 0.0647H^{0.8959}D^{1.4880}$	$W = W_R + W_C + W_S$	0.5201
Soft broadleaf	$W = 0.0459H^{0.1067}D^{2.0247}$	$W = 0.0856D^{1.2266}L^{0.3970}$	$W = 0.0444H^{0.71969}D^{1.7095}$	$W = W_R + W_C + W_S$	0.4956
Bamboo	$W = 0.3710H^{0.1357}D^{0.9817}$	$W = 0.2800D^{0.8357}L^{0.2740}$	$W = 0.0398H^{0.5779}D^{1.8540}$	$W = W_R + W_C + W_S$	0.5042
Shrub	/	/	/	$W = 0.4098H^{0.5427}D^{1.0615}$	0.5000
Herb	/	/	/	$W = 0.0549H^{0.8030}G^{1.0877}$	0.3998

W: Total biomass (kg); Shrub biomass model, H: height (m), D: ground diameter (cm); Herb biomass model, H: herbal average height (cm), G: coverage (%); the rest biomass models, H: Tree height (m), L: Crown length (cm), D: Diameter at breast height (cm).

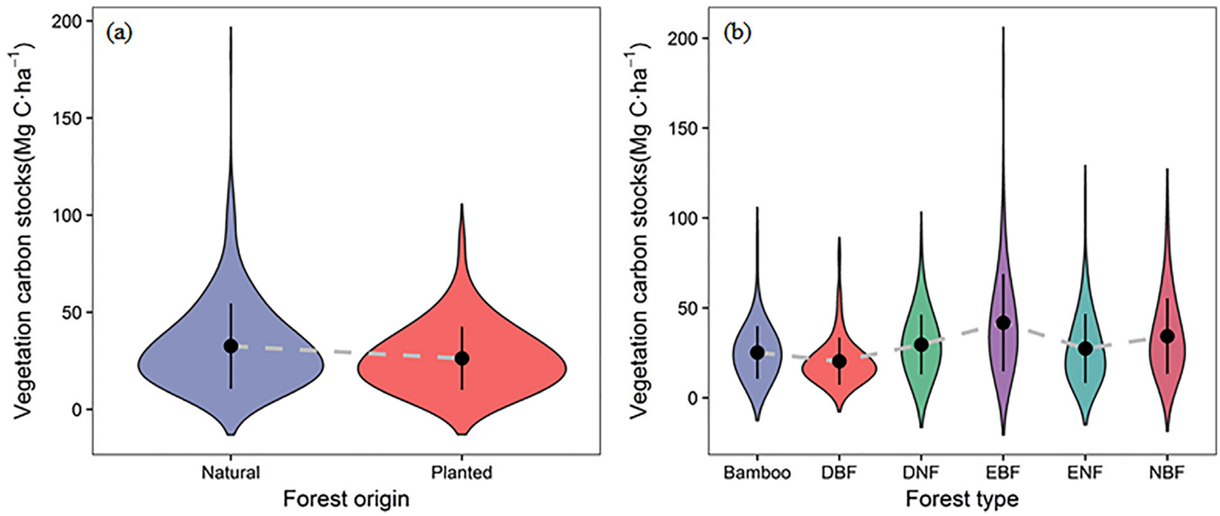

Fig. 2. The kernel density estimation of vegetation carbon stocks with different forest origin (a) and forest types (b). Black point represents the mean distribution value, and black line represents the SD of the distribution.

mean square residual (SRMR). Requirements for the best model included an insignificant χ^2 test statistic ($P > 0.05$), which indicates that sample and observed covariance matrices are statistically indistinguishable, SRMR <0.08, and both GFI and CFI > 0.95 (Grace et al., 2016; Hoyle, 2012). We also tested the expression of the collinearity of model according the path coefficient, correlation coefficient and determination coefficient (Kock and Lynn, 2012). Furthermore, we calculated the direct and indirect effects of the main driving factors on vegetation carbon stocks. All the SEM analyses performed using AMOS 21.0 (AMOS IBM, USA).

3. Results

3.1. Vegetation carbon stocks in subtropical forest ecosystems and relationship between abiotic/biotic factors and vegetation carbon stocks

Vegetation carbon stocks varied from 0.42 Mg C ha^{-1} to 182.12 Mg C ha^{-1}, with a median value of 32.20 Mg C ha^{-1}. The average vegetation carbon stocks in natural forests were larger than that in planted forests ($p < 0.001$) (Fig. 2a). The coefficient of variation of vegetation carbon stocks were larger in planted forests than in natural forests. Mean vegetation carbon stocks in forest types were 20.28 Mg C ha^{-1} (DBF), 25.19 Mg C ha^{-1} (Bamboo), 27.35 Mg C ha^{-1} (ENF), 29.57 Mg C ha^{-1} (DNF), 34.29 Mg C ha^{-1} (NBF), and 41.72 Mg C ha^{-1} (EBF) (Fig. 2b). Mean vegetation carbon stocks in age groups were 25.19 Mg C ha^{-1} (Bamboo), 29.44 Mg C ha^{-1} (Young), 31.62 Mg C ha^{-1} (Middle-age), and 34.06 Mg C ha^{-1} (Mature). Across all forest plots, vegetation carbon stocks significantly increased with forest age ($p < 0.001$) (Fig. 3).

Vegetation carbon stocks correlated positively with humus layer thickness, litter thickness, altitude, canopy density, vegetation coverage, and the ratio of C to N in leaf (Fig. 4). It was important to notice that canopy density and average age can explained 28% and 13.4% of the variation in vegetation carbon stocks.

3.2. Random Forest analysis and SEM: the main drivers of vegetation carbon stocks

Random Forest analysis indicated that canopy density, average age, litter thickness, forest type, altitude, vegetation coverage, land use

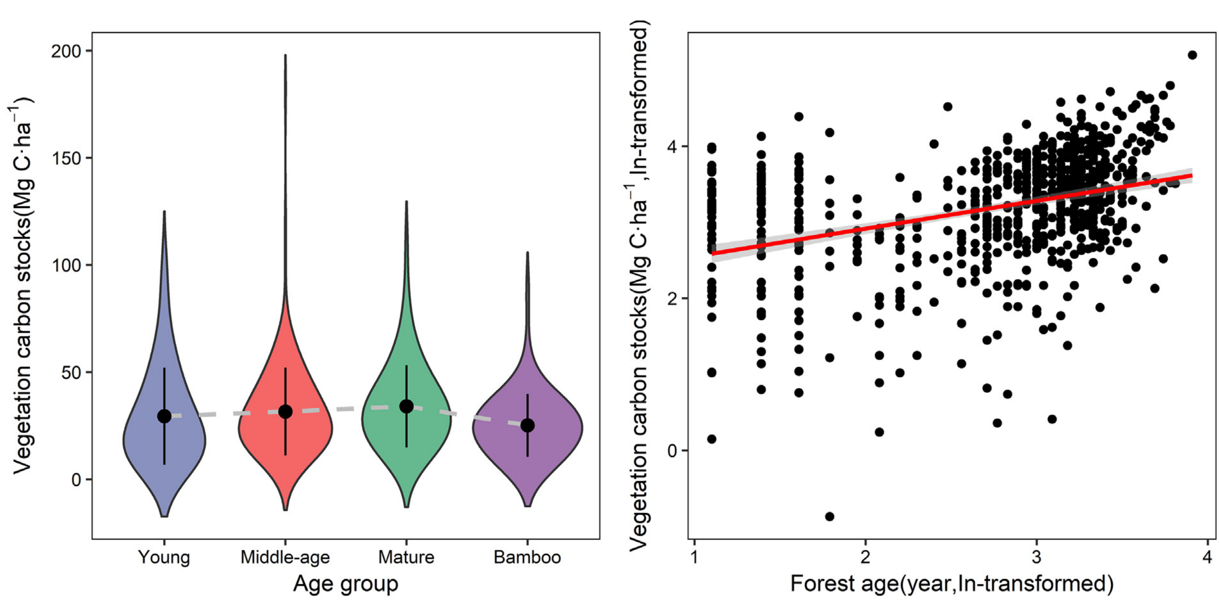

Fig. 3. Vegetation carbon stocks in different age groups (a) and as a function of forest age across all forests (b). Shaded areas show the 95% confidence interval of the fit.

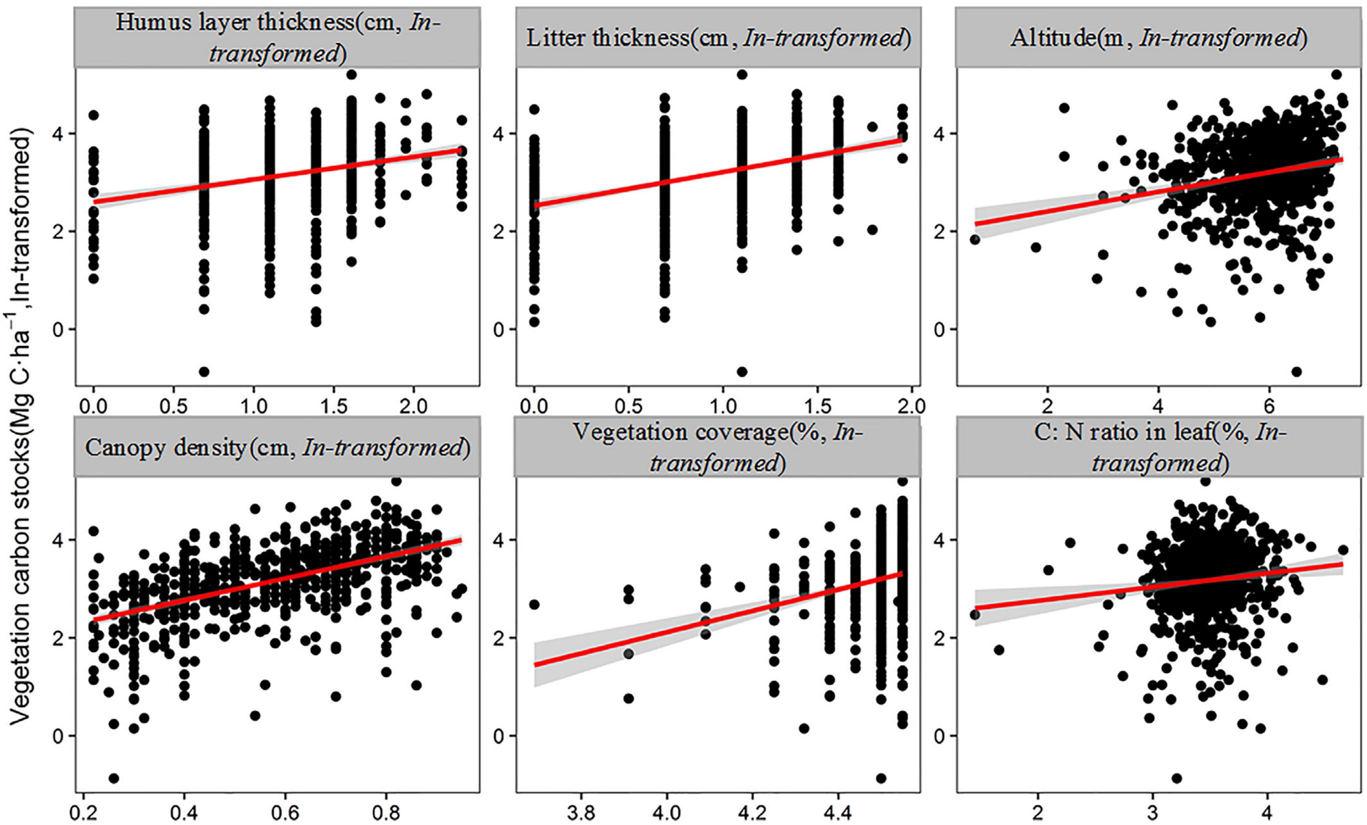

Fig. 4. Relationship between vegetation carbon stock and humus layer thickness (a), litter thickness (b), altitude (c), canopy density (d), vegetation coverage (e), and the ratio of C to N in leaf (f). Shaded areas show the 95% confidence interval of the fit.

type and age group were the most important predictors of vegetation carbon stock (Fig. 5). The importance of each driving factors decreased in the order: 76.39% (canopy density) > 47.25% (average age) > 21.93% (litter thickness) > 19.52% (forest type) > 18.95% (altitude) > 16.67% (land use type) > 15.46% (age group) > 14.83% (vegetation coverage). We found that canopy density and forest age were more important than other driving factors for vegetation carbon stocks. Random Forest analysis explained 50% of the variation in vegetation carbon stocks, in which canopy density accounted for 17.9% of the variation, and forest age accounted for 7.0%.

The SEM explained 52% of the variation in vegetation carbon stocks (Fig. 6). Altitude, canopy density, average age, and litter thickness had significantly direct positive effects on vegetation carbon stocks, in which the standardized direct effects were 0.173, 0.469, 0.406 and 0.144, respectively. Meanwhile, forest types and vegetation coverage had no direct effects on vegetation carbon stocks. But forest type presented indirect effects on vegetation carbon stocks by negatively affecting average age. Similarly, vegetation coverage presented indirect effects on vegetation carbon stocks by negatively affecting average age. The standardized total effects of each driving factor decreased in the order: 0.469 (canopy density) > 0.327 (average age) > 0.181 (altitude) > 0.144 (litter thickness) > 0.011 (vegetation coverage) > −0.1 (forest type) (Fig. 7). The results of standardized total effects indicated that canopy density and average age were the most important direct and indirect driving factors of vegetation carbon stocks.

4. Discussion

To understand the driving factors of vegetation carbon stocks in subtropical forest ecosystems, we used Random Forest analysis to assess relationships between abiotic and biotic factors and vegetation carbon stocks, and structural equation modeling (SEM) to evaluate the direct and indirect effects of the main driving factors.

4.1. Effects of biotic factors on vegetation carbon stocks

Both the Random Forest analysis and SEM showed that the importance and standardized total effects of canopy density were greater than those of other biotic factors, indicating that canopy density was the major biotic factor in modulating the vegetation carbon stocks in subtropical forest ecosystems. Canopy density is determined by the structural characteristics of canopy, species composition and stand attributes, such as diameter at breast height (DBH), stem density, and tree height. Stand structure is associated with differences in species composition, and there is a positive relationship between functional and

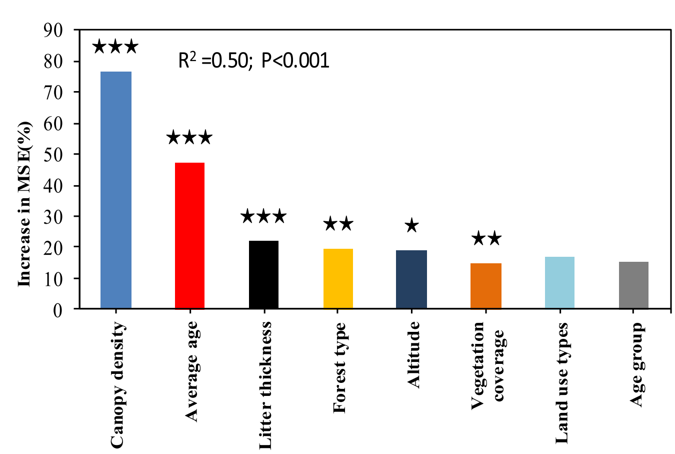

Fig. 5. Main predictors of vegetation carbon stocks. The figure shows the Random Forest mean predictor importance (% of increase in MSE) of abiotic and biotic drivers of vegetation carbon stocks. Statistical significance levels denoted as ⋆ = p < 0.05, ⋆⋆ = p < 0.01 and ⋆⋆⋆ = p < 0.001.

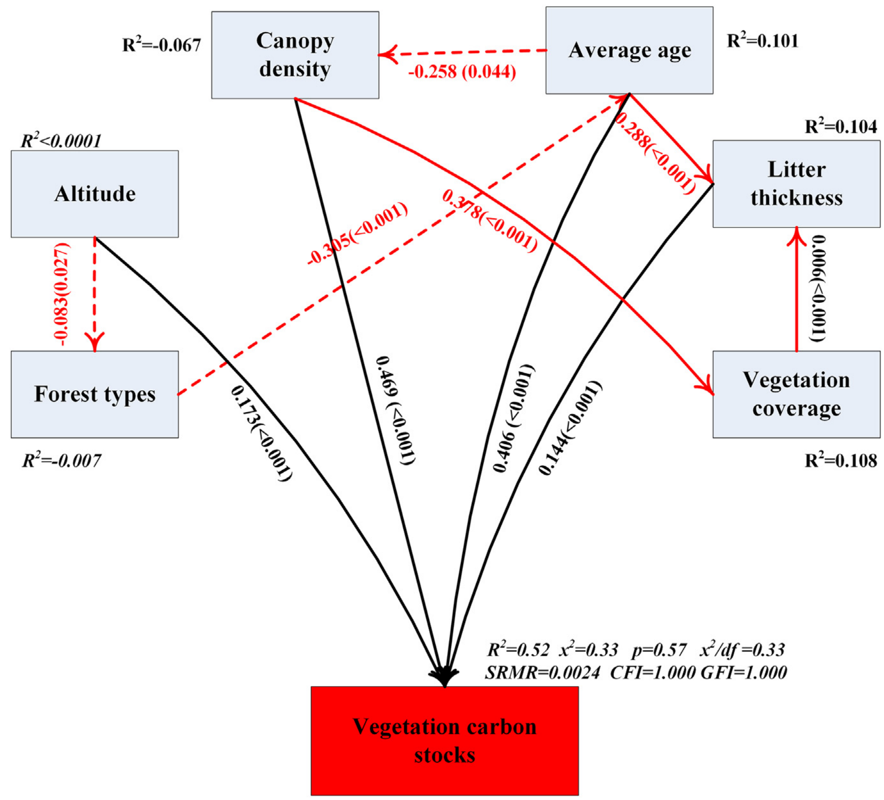

Fig. 6. Structural equation model of vegetation carbon stocks. Numbers adjacent to arrows indicate the effect-size (p value) of the relationship. Continuous black arrows indicate direct positive effects. Red arrows and dashed red arrows indicate indirect positive and negative effects, respectively. R^2 denotes the proportion of variation explained. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

taxonomic species diversity and aboveground biomass (Fotis et al., 2017). The structural characteristics of canopy are largely determined by species composition (Dial et al., 2004; Jucker et al., 2015) that has important consequences for forest productivity. Recent studies have shown that stem density (Chiang et al., 2016; M.H. Xu et al., 2017) and tree size (Ali et al., 2017; Zhang and Chen, 2015) increase with species diversity, which has strong direct effects on aboveground biomass. In the moso bamboo forests, the change in aboveground carbon stock did not correlate with environmental factors, but significantly increased with increasing culm density and average DBH (M.H. Xu et al., 2017; Xu et al., 2018). All this implies that canopy density is the main determinant of vegetation carbon stocks in subtropical forest ecosystems.

Forest age was another dominant factor in modulating the vegetation carbon stocks. The vegetation carbon stocks increases with stand

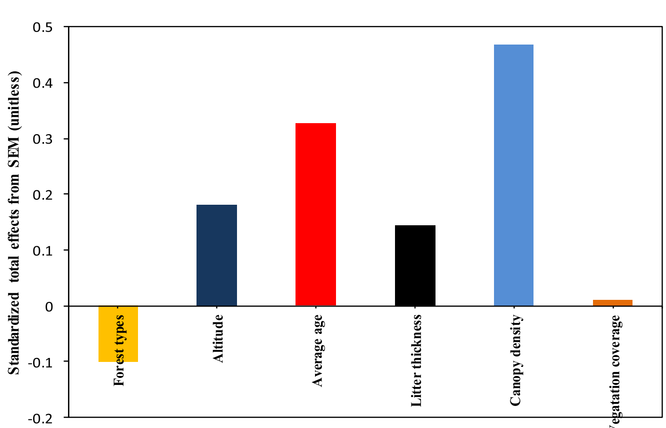

Fig. 7. Standardized total effects (direct plus indirect effects) derived from the SEM in Fig. 6.

development (Cheng et al., 2015; Fonseca et al., 2011). For instance, in a natural vegetation succession, carbon storage in biomass increased from grasslands to primary forests (Liu et al., 2016). Owing to nutrient limitation, stomatal constraint and declines in photosynthesis during the stand development, stand net primary productivity (NPP) declines along with the increase of tree age (Gower et al., 1996; McDowell et al., 2002; Tang et al., 2014). Furthermore, in agreement with Wang et al. (2017) who found that forest age was the main determinant of vegetation carbon turnover times across all forest types, forest age was the second most important driving factor of carbon stocks in our study.

In summary, canopy density and forest age accounted for 24.9% of the variation in the vegetation carbon stocks, and acted as the dominant determinants of vegetation carbon stocks in subtropical forest ecosystems. Compared with previous studies, our study increased the understanding of the main driving factors on vegetation carbon stocks by revealing and evaluating the direct and indirect effects of driving factors on vegetation carbon stocks. On the one hand, the direct effects of canopy density and forest age explained more variation in vegetation carbon stocks than those of other abiotic and biotic factors. On the other hand, canopy density and forest age indirectly affected vegetation carbon stocks by substantially affecting the other abiotic and biotic factors.

4.2. Effects of abiotic factors on vegetation carbon stocks

The importance and standardized total effects of altitude were higher than those of other abiotic factors in subtropical forests in Zhejiang. Both the Random Forest analysis and SEM showed that altitude was the most important abiotic driving factor of vegetation carbon stocks. Altitude can affect forest canopy, stem density and stand basal area, and thus indirectly affect aboveground biomass. The tree height usually decreases while the stem density increases with the increase in elevation (Girardin et al., 2013; Imani et al., 2017). Moreover, altitude

can affect aboveground biomass through regulating moisture and soil water availability (Fisk et al., 1998), which can significantly affect the biomass growth. The altitude gradient is associated with changes in precipitation, temperature, productivity and plant community type (Sanaei et al., 2018). Namgail et al. (2012) reported that the aboveground biomass increased with increasing altitude until 4400 m, and decreased with further increase in altitude. Ensslin et al. (2015) reported an increase in biomass with increasing altitude in altitudes lower than 2500 m. Similarly, in our study where altitude ranged from two to 1530 m, the vegetation carbon stocks increased with increasing altitude.

Fan et al. (2012) and Moeslund et al. (2013) reported that carbon storage and plant productivity were significantly affected by slope aspect and slope position. Contrary to that, we found no significant relationship between other abiotic factors and vegetation carbon stocks, possibly due to the finding that vegetation carbon stocks in forest ecosystems did not correlate with environmental factors on a large regional scale (M.H. Xu et al., 2017). Furthermore, the influence of environmental factors on vegetation carbon stock may be masked by the temporal and spatial heterogeneity on the large area scale.

4.3. Large potential for increasing vegetation carbon stocks

The mean vegetation carbon stocks in forest types ranged from 20.28 Mg C ha^{-1} in deciduous broadleaf forest to 41.72 Mg C ha^{-1} in evergreen broadleaf forest, and the overall average was close to the average carbon stock of 31.85 Mg C ha^{-1} in ecological service forests in Zhejiang, China (Zhang et al., 2007). Compared to previous studies in similar forest types in China, Japan, Europe, and the United States at similar latitudes (Fang and Chen, 2001; Iwaki, 1983; Dixon et al., 1994; Turner et al., 1995), the mean vegetation carbon density in Zhejiang was lower. The carbon stocks were also much lower than the global average value. Almost 90% of the stands in our study were younger than 20 years (Zhang et al., 2007), which may be the main reason for the low average carbon stocks. The low vegetation carbon stocks indicated that the subtropical forest ecosystems in Zhejiang have a large potential for increasing vegetation carbon stocks.

In our study, the average vegetation carbon stocks were larger in natural forests than in planted forests, possibly because planted forests and natural forests have different biomass allocation patterns. Plants usually allocate more biomass to roots than to foliage with plant growth (Shipley and Meziane, 2002). Also, planted forests are usually young forests with fast-growing species that allocate more biomass to foliage to compete for light availability, whereas natural forests are generally old forests that must allocate more biomass to roots and stems to support their standing (Peichl and Arain, 2007). This lead to a relatively longer vegetation carbon turnover times in natural forests than that in planted forests (Wang et al., 2017), thereby to larger carbon stocks in natural forests.

5. Conclusion

To our knowledge, this is the first empirical study to evaluate the abiotic and biotic driving factors of vegetation carbon stocks in subtropical forest ecosystems using the Random Forest analysis and structural equation modeling (SEM). Random Forest analysis identified the most important driving factors of vegetation carbon stocks. With SEM we tested whether the relationship between driving factors and vegetation carbon stocks was maintained when the driving factors were taken into account simultaneously. The approaches provided complementary insights on the factors that driving vegetation carbon stocks at a large scale.

The average vegetation carbon stocks were lower than the average level of similar forest types in China and worldwide at similar latitudes, implying that the forest ecosystems in our study have large carbon sequestration potential. According to the Random Forest analysis, 50% of the variation in vegetation carbon stocks could be explained by biotic and abiotic factors, among which canopy density accounted for 17.9%, and forest age accounted for 7.0% of the total variation. The SEM explained 52% of the variation in vegetation carbon stock. Canopy density and forest age with the standardized total effects of 0.469 and 0.327, respectively, were the most important direct and indirect driving factors of vegetation carbon stocks. Our study increases the understanding of vegetation carbon sequestration in subtropical forest ecosystems and may benefit to subtropical forest management.

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Author contributions

The analysis were performed by Lin Xu, Yongjun Shi and Huiyun Fang. All authors contributed with ideas, writing, revising, and discussion.

Conflicts of interest

The authors declare no conflict of interest.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2018.03.080.

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